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MODERN DISTRIBUTION PATTERNS OF SNAILS AND PLANTS IN THE WESTERN CARPATHIAN SPRING FENS: IS IT A RESULT OF HISTORICAL DEVELOPMENT?

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ABSTRACT

The aims of the study were: (1) to investigate the modern distribution pattern of snails in the Western Carpathians (Czech Republic and Slovakia) and compare it with the modern distribution pattern of plants, in which a conspicuous species turnover occurs on the scale of only tens of kilometres; and (2) to construct an hypothesis explaining why such a steep geographical gradient exists in such a small area, which is homogenous with respect to water chemistry and climate. Snail assemblages of 111 treeless base-rich spring-fen sites were sampled quantitatively from a homogeneous area of 16 m^2 (one sample of 12 l volume) in which a vegetation relevé was also recorded. The result of a partial detrended correspondence analysis of snail data with water pH and conductivity as co-variables confirmed clear differences between snail assemblages of the study area's western and eastern region. The regions differed in their species pool and the frequencies of particular species. In the eastern region, fen specialists and relics occurred and they were fairly frequent and abundant (e.g. *Vertigo geyeri* and *Pupilla alpicola*). The western region differed by its higher frequency and abundance of woodland and ubiquitous species. The classification of snail species based on their co-occurrence with plant species reflected the known geographical pattern as well. We found that Western Carpathian fen vegetation as well as the fens' snail assemblages display a clear geographical gradient within a rather small area, independently of any climate or other environmental variation. Previously published palaeoecological data and both species composition and structure of modern assemblages suggest clear differences in the historical development of the two principal regions. Historical development seems to be one of the most important variables constituting qualitative characters of modern fragmented communities. On a small scale it can influence especially organisms with slower migration rates, such as molluscs.

INTRODUCTION

The variation in plant and animal assemblages on a large scale reflects geographical patterns of species distributions. Climate-related gradients are responsible for some of this variation (Archibold, 1995), but historical factors are also significant. To take history into consideration is important for understanding recent species distribution and occurrence (e.g. Meyrick & Preece, 2001), because the evolution of modern communities and distribution patterns has been mostly governed by the environmental changes and human activities during the Holocene (Huntley & Birks, 1983; Ložek, 2000; Cubizolle *et al.*, 2003; Rowe *et al.*, 2004). On a smaller scale, the roles of soil conditions such as moisture, pH and nutrient availability become more important. Historical effects can only be inferred when large- and small-scale environmental variation is not associated with distribution.

The plant communities of base-rich spring fens in the western part of the Western Carpathians display a unique geographical gradient. A partial, but clear species turnover has been observed on the scale of only tens of kilometres, independently of any climate or other environmental variation. Base-rich fens in the eastern region, i.e. limestone Inner Western Carpathians and the Orava region with flysch bedrock (Fig. 1A), harbour many rich-fen species that penetrate westwards only slightly or not at all. Species such as *Primula farinosa, Carex lepidocarpa, C. hostiana, C. dioica, Pinguicula vulgaris, Schoenus ferrugineus* and *Pedicularis sceptrum-carolinum*, so typical of the Inner Carpathian calcareous fens, are nearly completely absent in the western and northernmost parts of the Western Carpathians (Hájek, 1999; Hájek & Háberová, 2001). By analogy, some poor fen and moderately rich fen species as *C. magellanica, C. chordorrhiza* and *C. limosa* (Dítě & Pukajová, 2002, 2003) or the mosses *Paludella squarrosa* and *Meesia triquetra* (e.g. Šoltés, 1997) have a clear distribution centre in the central part of the Northern Carpathians. None of these species reaches its western distribution limit there. Such a marked geographical difference cannot be explained by the ecological conditions of fens. None of the major factors generally controlling species distribution in fens (base richness, nutrient availability, water regime, altitude) differs between the western and eastern calcareous fens in the westernmost Carpathians (Hájek, 2005). These facts suggest that there might be some historical reasons connected with the extent of historical distribution of fen habitats and with migration relationships. One way of elucidating the underlying processes forming this gradient is to investigate a completely different taxonomical group. Land shelled gastropods (called snails below) seem to be suitable organisms for such a comparative study, because their site occurrence is controlled by similar factors as in plants (Horsák & Hájek, 2003), although they are not trophically connected with them on the species or genus level as, for example, are many phytophagous insects. Snails are predominantly herbivorous, mainly feeding on decaying

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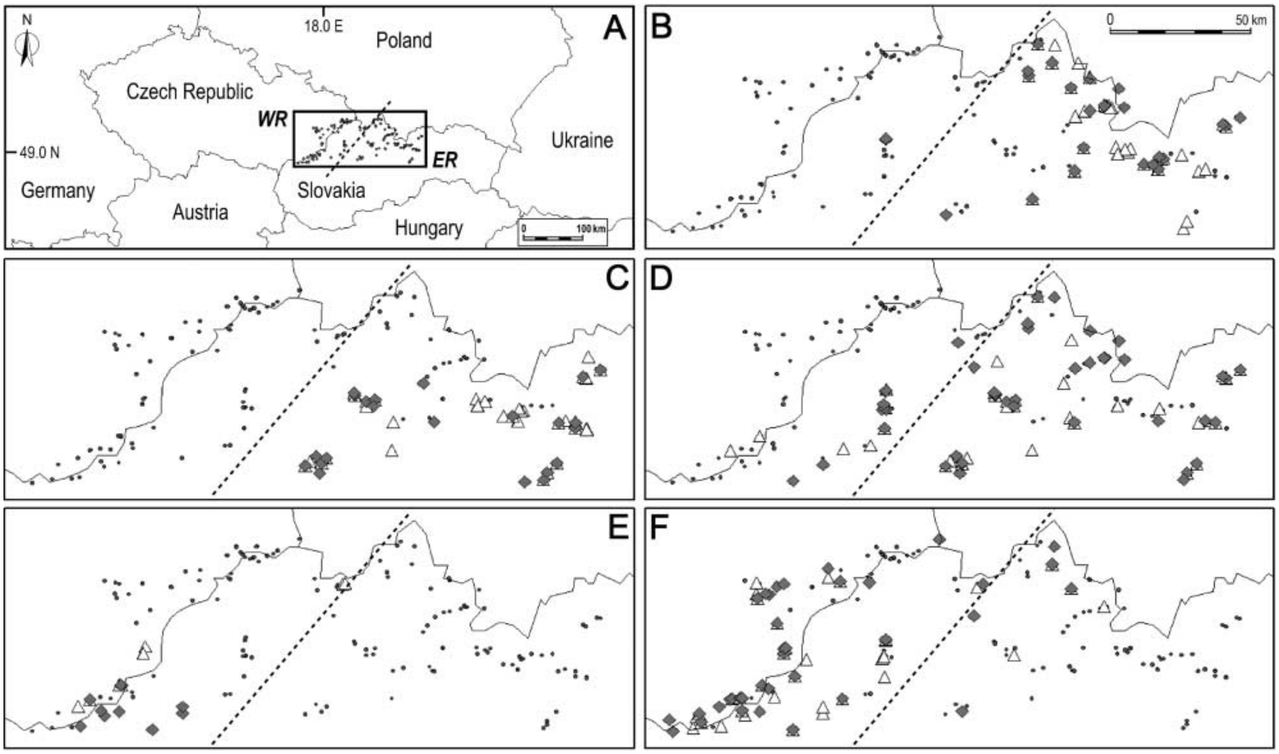

Figure 1. Location of study area with the position of all study sites (**A**) and distribution maps of species differing the most in their occurrence between the WR and ER. **B**–**E** are the most correlating snail (diamonds)–plant (triangles) pairs: **B.** *Vertigo geyeri* (diamonds) and *Carex dioica* (triangles). **C.** *Pupilla alpicola* (diamonds) and *Primula farinosa* (triangles). **D.** *Euconulus praticola* (diamonds) and *C. lepidocarpa* (triangles). **E.** *V. moulinsiana* (diamonds) and *Equisetum telmateia* (triangles). **F.** Distribution of two common forest snails in the studied fens: *Monachoides incarnatus* (diamonds) and *Aegopinella pura* (triangles). All co-occurrences but *V. moulinsiana*–*E. telmateia* were significant (using Bonferroni correction the cut level was $P = 0.000003$).

matter and withering parts of plants (e.g. Cameron, 1978; Speiser, 2001), but without any evidence of relationships on the species level (i.e. monophagy).

The aims of this study are: (1) to investigate modern distribution pattern of snails in the Western Carpathians; (2) to compare it with modern distribution pattern of plants; and (3) to construct a hypothesis for explanation why such a steep geographical gradient exists within a rather small area.

MATERIAL AND METHODS

Study area and study sites

The study of 111 base-rich spring fen sites was carried out in the Western Carpathians (Fig. 1A). The study area consists of two principal regions that differ in the species composition of plant communities. The first one includes the Moravian–Slovakian borderland between the Czech Republic and Slovakia plus adjacent regions (called western region, WR, 56 sites, Fig. 1A) and is located on the western margin of the Western Carpathians. The second one is the western part of the Inner Western Carpathians and the neighbouring Orava region (called eastern region, ER, 55 sites, Fig. 1A).

The geological structure of the study area is rather complicated. The westernmost and northernmost parts are composed of flysch bedrock with sandstone and claystone alternating in each geological stratum (bed). The beds differ from each other both in chemistry and the proportion of sandstone and claystone. Each bed mostly occupies a narrow strip stretching from southwest to northeast (Poprawa & Nemčok, 1988); the Klippen Belt with abundant limestone forms the nearest strip stretching along the outer edge of the Inner Western Carpathians. The chemical composition of groundwater reflects the rock chemistry (Rapant, Vrana & Brodiš, 1996). Groundwater chemistry varies from carbonatogenic waters, which support cold-water travertine (tufa) formation (in the south), to acid ones, which are rich in iron, silicates and sulphates and poor in all other elements (in the northernmost part of the Moravian–Slovak borderland). The remaining part of the study area, mostly WR, typically contains cores of Paleozoic and crystalline schists overlain by Mesozoic shale-sandstone and carbonate lithofacies (limestone, dolomite). These are covered by the Inner Carpathian Paleogene or by the Neogene layers. Thus, groundwater conditions vary, depending on the bedrock chemistry. The limestone and the Paleogene aquifers have groundwater similar in chemical composition to that of the flysch belt (Hájek & Hekera, 2005).

The study sites were treeless sloping spring fens, which covered nearly the entire variability of fens along the main poor–rich trophic gradient (Malmer, 1986; Hájek, Hekera & Hájková, 2002; Horsák & Hájek, 2003). The five following vegetation types represent the most common fen habitats (arranged from mineral-richest to mineral-poorest): (1) travertine swards (the *Glauco–Trichophoretum pumili* association); (2) extremely rich tufa-forming fens (the *Carici flavae–Cratoneuretum* association); (3) calcareous peat-forming fens (the *Caricetum davallianae* association); (4) extremely rich peat-forming fens (the *Valeriano simplicifoliae–C. flavae* association); (5) moderately calcium-rich *Sphagnum*-fens (the *Sphagno warnstorfii–Tomenthypnion* alliance). For species composition of the above-mentioned vegetation, see Valachovič (2001) and Hájek *et al.* (2005).

Sampling methods

Fieldwork was conducted from 2000 to 2004. In each site, one sample of 12 l volume comprising the upper soil layer including litter, bryophytes and herbaceous vegetation was collected in order to sample snail assemblages. The samples were washed through a bowl-shaped sieve (mesh size 0.5 mm) to wash out the fine clay particles (otherwise they would have caused all the material to stick together after drying). The coarse plant matter was removed by hand. This method is described in detail by Horsák (2003). After drying, the material was separated by sieving into fractions of different particle size, from which the shells were extracted by hand-sorting under a binocular microscope. Samples were not collected randomly, as the material collected was meant to reflect the area (16 m^2), homogeneous in terms of vegetation composition and structure, in the central part of the site. The primary goal was always to detect the site's species as exhaustively as possible. Mollusc species names are given according to Juřičková *et al.* (2001), except *Euconulus alderi* (Gray, 1840), for which the name *E. praticola* (Reinhardt, 1883) is used (Falkner, Ripken & Falkner, 2002). The species composition of the vascular plants and bryophytes was recorded in the same 16 m^2 (4 × 4 m) plots. The cover of each plant species was estimated using a nine-grade scale (van der Maarel, 1979). The plant names follow Marhold (1998) for vascular plants and Frey *et al.* (1995) for bryophytes.

Water conductivity and pH were measured in the microsites best supplied by water in small shallow holes dug in the central part of the spring fen, using portable instruments with automatic temperature compensation (CM 101 and PH 119, Snail Instruments, Beroun, Czech Republic). The readings were standardized to 20°C. Conductivity was measured to indirectly approximate water mineral richness, especially Ca + Mg concentration (cf. Sjörs & Gunnarsson, 2002; Hájek *et al.*, 2005).

Statistical analyses

Only live specimens and empty shells with entire periostracum were used for the analyses. Species of which no live specimen was found in any of the sites were omitted because these were inhabitants of adjacent habitats, which do not live in fens. In total, 4422 records of 353 plant species and 1135 records of 49 snail species were analysed. In total, material consisting of more than 11,000 snail specimens was analysed.

Mollusc data were square-root transformed and processed by partial detrended correspondence analysis (partial DCA) with water pH and conductivity as co-variables. For each snail species, probability of non-random co-occurrence with each plant and each snail species was calculated by Fisher's exact test, using the JUICE software (Tichý, 2002). For this calculation only presence/absence data were used. The obtained values were recalculated as −log(value of Fisher's exact test) and this new value represented fidelity of co-occurrence of species. The higher the values yielded by the computation, the higher the fidelity of plant or snail species to the target snail species (for details see Chytrý *et al.*, 2002).

The resulting snails-by-plants species matrix was classified by cluster analysis (Ward's method, Euclidean distance). Due to high variation of fidelity values (from 10^{-16} to 12.41), a square-root transformation was used in order to reduce the influence of dominants. In order to find plant indicators of individual snail clusters, indicator species analysis was done (Dufrêne & Legendre, 1997) using the PC-ORD package (McCune & Mefford, 1999). The same matrix was subjected to principal component analysis (PCA) and results of the cluster analysis were projected into the PCA ordination diagram. Two supplementary factors were also projected into the PCA ordination diagram, in order to interpret the first two PCA axes. The first factor was an index of differences between particular species frequency in the western and in the eastern part (IDF, Index of Different Frequency) calculated as:

$$\mathrm{IDF} = \frac{(\mathrm{W} - \mathrm{E})/(\mathrm{W} + \mathrm{E}) + 1}{2} \qquad (1)$$

where W, E are frequencies of particular species in the western (W) and in the eastern (E) region of the study area. The index is defined in an interval of 0 to 1. The second factor expressed the individual species demands for calcium. It was calculated as a median value of water conductivity (corresponding well with calcium concentration, see Horsák, 2006) for the sites where the target species occurred (MCS, Median Conductivity of Sites).

The CANOCO 4.5 package was used for ordination techniques (ter Braak & Šmilauer, 2002).

RESULTS

Geographical pattern in species composition of snail assemblages

The result of partial DCA analysis (Fig. 2) confirmed clear differences in snail assemblages between the two geographical regions. The sites were nearly completely separated along the first axis in the partial DCA diagram with a rather narrow overlap zone. This variation is caused both by different species pools and by frequencies of some common species (Table 1). Two species, recorded in more than 10 sites, whose occurrences were limited exclusively to a particular geographical region, were encountered, *Vertigo moulinsiana* in the western region (Fig. 1E) and *Pupilla alpicola* in the eastern region (Fig. 1C). Far more species significantly differed in frequency between the two studied regions. In the eastern region fen specialists were more commonly present: e.g. *V. geyeri* (Fig. 1B), *Euconulus praticola* (Fig. 1D) and *Perpolita petronella*, whereas in the western region woodland and ubiquitous species were more frequent, for example *Aegopinella pura*, *Monachoides incarnatus* (Fig. 1F) and *E. fulvus*.

Classification of snails based on their co-occurrence with plants

We obtained 826 significant ($P < 0.05$) co-occurrences between snails and plants; 28 of them were significant also using Bonferroni

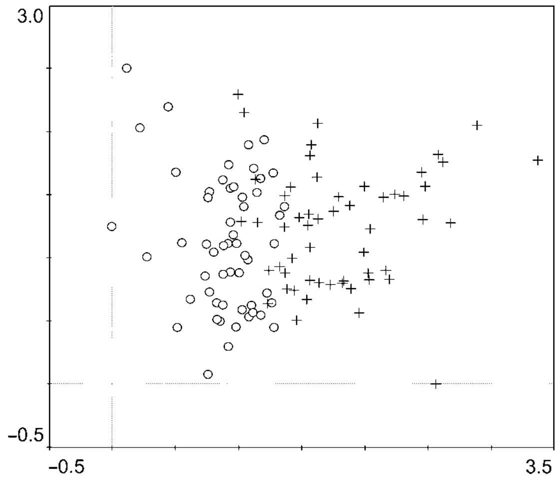

Figure 2. Partial DCA of mollusc assemblages (with water pH and conductivity as co-variables): ordination plot of sites on the first two DCA axes. Sum of all eigenvalues was 1.326. The eigenvalue of the first ordination axis was 0.289, and that of the second axis was 0.131. Percentage variance of the species data explained by the first axis was 21.8%, that by the second axis was 9.9%. Classification of investigated sites based on their position: WR, circles; ER, crosses.

Table 1. List of mollusc species found in more than 10 sites within the whole area under study.

Ecological group		Species	WR	ER	Differ.	IDF	*P*
1	SI	*Platyla polita* (Hartmann, 1840)	12	9	3	0.5714	0.3309
		Acanthinula aculeata (O.F. Müller, 1774)	15	0	**15**	**1.0000**	<**0.0001**
		Vitrea diaphana (Studer, 1820)	14	4	10	0.7777	0.0104
		Aegopinella pura (Alder, 1830)	28	6	**22**	**0.8235**	<**0.0001**
		Daudebardia rufa (Draparnaud, 1805)	22	5	**18**	**0.8333**	**0.0002**
2	SI (MS)	*Monachoides incarnatus* (O.F. Müller, 1774)	31	6	**25**	**0.8378**	<**0.0001**
		Arianta arbustorum (Linné, 1758)	8	3	5	0.7272	0.1070
	SI (HG)	*Vitrea crystallina* (O.F. Müller, 1774)	8	8	0	0.5000	0.5909
3	SIi	*Perforatella bidentata* (Gmelin, 1791)	9	9	0	0.5000	0.5849
5	PT	*Vallonia pulchella* (O.F. Müller, 1774)	44	44	0	0.5000	0.5195
		Vertigo pygmaea (Draparnaud, 1801)	48	21	**27**	0.6956	<**0.0001**
	PT(SI)	*Vallonia costata* (O.F. Müller, 1774)	22	4	18	**0.8461**	<**0.0001**
7	MS	*Cochlicopa lubrica* (O.F. Müller, 1774)	56	42	14	0.5714	<**0.0001**
		Punctum pygmaeum (Draparnaud, 1801)	50	34	**16**	0.5952	**0.0007**
		Euconulus fulvus (O.F. Müller, 1774)	49	21	**28**	0.7000	<**0.0001**
		Vitrina pellucida (O.F. Müller, 1774)	24	12	**12**	0.6666	0.0015
		Perpolita hammonis (Ström, 1765)	36	39	3	0.5200	0.2939
		Plicuteria lubomirskii (Ślósarskii, 1881)	20	4	**16**	**0.8333**	**0.0002**
8	HG	*Carychium tridentatum* (Risso, 1826)	42	23	**19**	0.6461	**0.0004**
		Columella edentula (Draparnaud, 1805)	27	14	13	0.6585	0.0108
		Vertigo angustior, Jeffreys, 1830	30	37	7	0.4477	0.0999
		Vertigo substriata (Jeffreys, 1833)	35	30	5	0.5384	0.2554
		Succinella oblonga (Draparnaud, 1801)	21	9	12	0.7000	0.0104
		Perpolita petronella (L. Pfeiffer, 1853)	1	10	9	**0.0909**	0.0037
9	PD	*Carychium minimum*, O.F. Müller, 1774	53	50	3	0.5145	0.3480
		Pupilla alpicola (Charpentier, 1837)	0	24	**24**	**0.0000**	<**0.0001**
		Vertigo antivertigo (Draparnaud, 1801)	48	37	11	0.5647	0.0187
		Vertigo geyeri, Lindholm, 1925	2	23	**21**	**0.0800**	<**0.0001**
		Vertigo moulinsiana (Dupuy, 1849)	11	0	11	**1.0000**	**0.0003**
		Succinea putris (Linné, 1758)	26	29	3	0.4727	0.3179
		Oxyloma elegans (Risso, 1826)	21	34	13	0.3818	0.0086
		Zonitoides nitidus (O.F. Müller, 1774)	15	12	3	0.5555	0.3491
		Euconulus praticola (Reinhardt, 1883)	8	36	**28**	**0.1818**	<**0.0001**

Abbreviations: 1 SI (SIL VICOLAE), strict forest species; 2 SI(MS), forest species frequently occurring in mesic habitats as well (such as gardens, parks, etc.); and in wet habitats SI(HG); 3 SIi, species of flood plain forests; 5 PT (PRATICOLAE), forest-avoiding species; PT(SI), some able to survive in shrubs; 7 MS (MESICOLAE), mesophilous and mostly euryoecious species; 8 HG (HYGRICOLAE), species with high moisture demands, but not confined to wetlands; 9 PD (PALUDICOLAE), extremely hygrophilous terrestrial species living in many types of wetlands.

The species were subjected to ecological classification according to Ložek (1964) and Lisický (1991) with small modifications. Number of records in the WR and ER are indicated. Difference of each species occurrence between the two mentioned regions (Differ.) and index of differences between particular species frequency in the western and in the eastern region (IDF, for details see Material and Methods) were calculated. Differences higher than 14 records and values of IDF lower than 0.25 or higher than 0.75 are given in bold. Fisher's exact test values are given in the last column and significant values are in bold (using Bonferroni correction the cut level was $P = 0.001$).

correction ($P < 0.000003$). Cluster analysis on the basis of Fisher's exact test values separated snail species into four basic clusters (Fig. 3). The result of the PCA analysis is in very good concordance with the result of the cluster analysis (Fig. 4).

The snail species were arranged along the first axis in the PCA diagram following the geographical gradient. On the left side (cluster 1) the species significantly more frequent in the western region were plotted (Table 1). This group of snails included many ubiquitous species (e.g. *Cochlicopa lubrica*), woodland species such as *Aegopinella pura* (Fig. 1F) and species preferring young and temporary open habitats (e.g. *V. pygmaea*). All these snail species had together 686 (12 per site) and 356 (six per site) records in the western and in the eastern region, respectively. Significant plant indicators of this cluster were mainly wet-meadow species (e.g. *Cirsium oleraceum*, *Anthoxanthum odoratum*, *Ajuga reptans*, *Briza media*), species of strongly petrifying calcareous springs without organic matter (*Cratoneuron commutatum*, *Carex flacca*) and the species of initial seepages on landslides (e.g. *Equisetum telmateia*). On the right side, the demanding and relic species (cluster 4) such as *V. geyeri* and *P. alpicola* were plotted (Fig. 4). These two snails are the only exclusive mollusc inhabitants of fens within the Western Carpathians. Significant plant indicators of this cluster were also refugial species such as *C. dioica*, *C. hostiana*, *Pinguicula vulgaris* and *Primula farinosa*. Snail species forming cluster 3 fell in the middle of the ordination plot as most of them occurred with similar frequencies in both regions. No significant plant indicator species was found. The second axis expressed calcicole–calcifuge behaviour of snail species. The most calcium demanding snail species were plotted in the lower part of the ordination plot. Three snail species with the lowest requirements for calcium formed cluster 2, which was placed in the upper part,

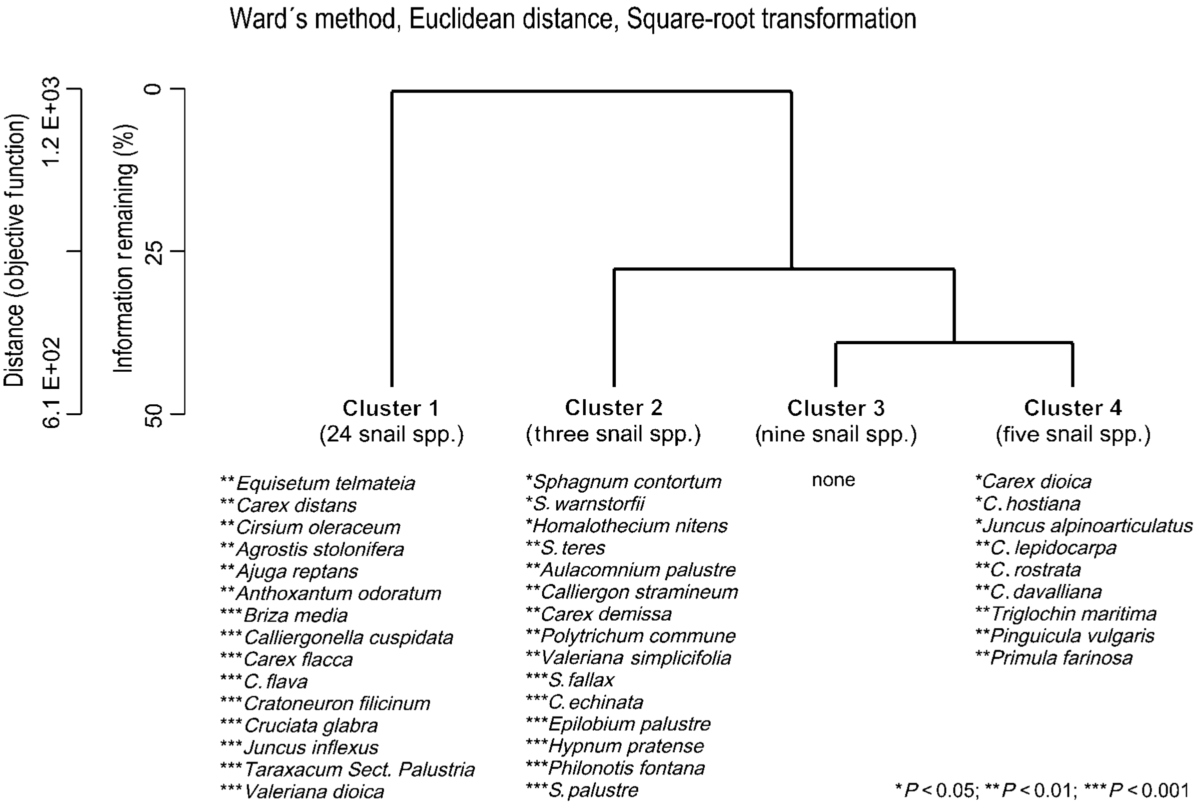

Figure 3. Cluster analysis of mollusc species based on their correlations with each plant species expressed as log-transformed probabilities of non-random co-occurrence determined by Fisher's exact test. Significant plant indicators are shown under each group.

separated far from the others along the second axis. Significant plant indicators of this cluster were species preferring or forming acid sites (i.e. peat mosses – *Sphagnum* sp. div.).

Similarities in occurrence of snail and plant species

Based on probabilities of non-random co-occurrence we found four snail–plant pairs of species well correlating in their occurrences, which are interesting from a historical point of view: *V. geyeri–C. dioica*, *P. alpicola–Primula farinosa*, *E. praticola–C. lepidocarpa* and *V. moulinsiana–E. telmateia* (Fig. 1B–E). These snail species were completely or nearly completely limited either to the western or eastern region and their occurrences were more correlated with the plant species than with any other snail species.

DISCUSSION

Our study shows that not only plant, but also snail assemblages may display a clear geographical gradient within a rather small area. On the basis of species composition of land snails, although the sites were generally well separated, there was a clear overlap zone. In this context, we note that not all sites in the eastern region were relic and/or harbouring relic species. Some eastern sites could be very young and thus be expected to have the same fauna as the western ones. The regions are contiguous, and some movement between them can occur. Thus some eastern sites (crosses) are found in the subset of western sites (circles) rather than *vice versa* (Fig. 2).

A priori, the most probable explanation of observed conspicuous alternation in species composition within such a relatively small area is the existence of some ecological gradient(s). Calcium content is generally known as the main controller of land snail species composition and it also has a strong effect on fen communities (Horsák & Hájek, 2003). Therefore, we assessed two good and commonly used proxies of calcium content, pH and conductivity, but no significant difference between studied regions was found ($P \gg 0.05$, Mann-Whitney *U* test). The possible existence of a climatic gradient could be another explanation for these differences. Although there are climatic differences between the studied regions, with the Inner Western Carpathians being colder and wetter, this difference is a product of including high mountain climates, in that region only, in the regional average. However, no studied sites were situated in high montane areas there (no base-rich fens occur at higher altitudes). Studied sites of both regions are situated in the basins, which climatically belong to the same unit – a moderately warm region (Quitt, 1971).

On the other hand, known palaeoecological data support a hypothesis of different historical development of these two regions. Published results show that the Outer Western Carpathian fens are much younger than the Inner Western Carpathian ones. The open fen-meadow state of the Outer Carpathian fens is quite young. It is the result of human activities, namely of an extensive deforestation during the largest Walachian colonization, which started 600–700 years ago (Horsák & Hájková, 2005; Rybníčková, Hájková & Rybníček, 2005). By contrast, at least some fens in the Inner Carpathians and in the Orava region represent relic habitats from the Boreal period (Jankovská, 1988; Rybníček & Rybníčková, 2003). These few profiles, mentioned above, are not sufficient for a reconstruction of the past environment of the whole region because they can represent cases of extreme site conditions. We assume that only a few recent sites in the Inner Carpathians have existed continuously in the present state.

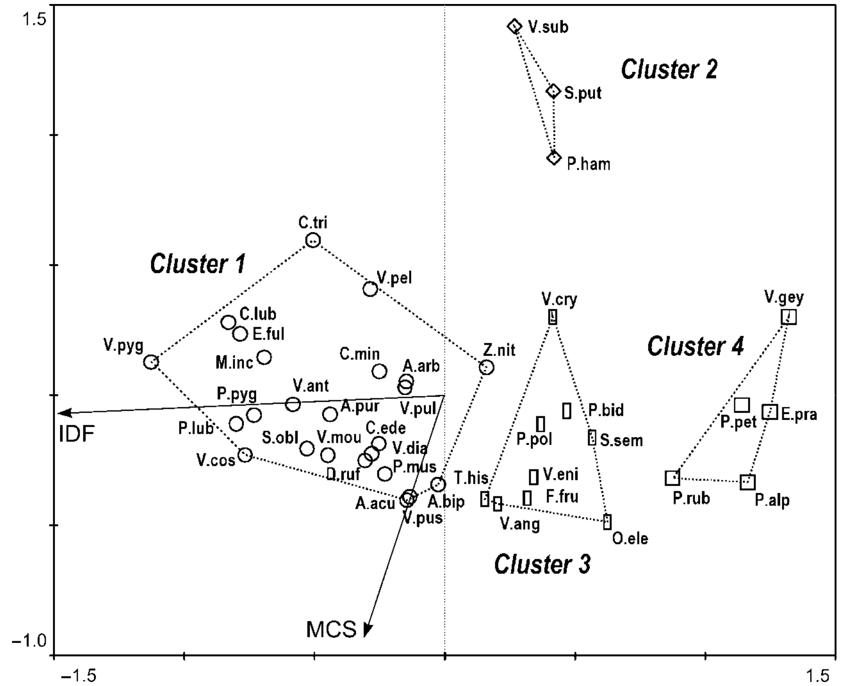

Figure 4. PCA: ordination plot of snail species on the first two PCA axes. The eigenvalue of the first PCA axis was 0.374, that of the second axis was 0.172. Percentage variance of the species data explained on the first axis was 37.4%, that on the second axis was 17.2%. The classification is based on cluster analysis (Fig. 3). Median value of conductivity for sites where the target species occurred (MCS) and index of differences between particular species frequency in the western and in the eastern region (IDF) were only passively projected into the ordination diagram. Species list in alphabetic order: *Acanthinula aculeata*, *Aegopinella pura*, *Alinda biplicata*, *Arianta arbustorum*, *Carychium minimum*, *C. tridentatum*, *Cochlicopa lubrica*, *Columella edentula*, *Daudebardia rufa*, *Euconulus praticola*, *E. fulvus*, *Fruticicola fruticum*, *Monachoides incarnatus*, *Oxyloma elegans*, *Perforatella bidentata*, *Perpolita hammonis*, *P. petronella*, *Platyla polita*, *Plicuteria lubomirskii*, *Pseudotrichia rubiginosa*, *Punctum pygmaeum*, *Pupilla alpicola*, *P. muscorum*, *Semilimax semilimax*, *Succinea putris*, *Succinella oblonga*, *Trichia hispida*, *Vallonia costata*, *V. enniensis*, *V. pulchella*, *Vertigo angustior*, *V. antivertigo*, *V. geyeri*, *V. moulinsiana*, *V. pusilla*, *V. pygmaea*, *V. substriata*, *Vitrea crystallina*, *V. diaphana*, *Vitrina pellucida*, *Zonitoides nitidus*.

An historical continuum has probably not existed within a particular site, but in the larger area as a spatial–temporal continuum. Therefore, it is very difficult to confirm the existence of the continuum using just palaeoecological evidence. Recent communities can reflect the spatial–temporal continuum better. Both approaches together can provide a more accurate estimation of the historical development.

Palaeorefugia versus neorefugia, influence on snail assemblage composition

Nekola (1999) proposed the concept of two types of biological refugia where the palaeorefugia are remnants of once-more-widespread distributions that have become fragmented, whereas the neorefugia represent a *de novo* development of habitats in a landscape where they were previously absent. The Western Carpathian fens are considered to be refugia, as they support communities and species unable to survive elsewhere in the landscape (*sensu* Pielou, 1979). The sites in the western region of the study area are all typical neorefugia. Their modern appearance is the result of human deforestation *ca.* 650 years ago. In general, they represent refugia on a community level. They also serve as refugia for individual plant species, but not for snails. This is probably due to the low migration ability of snails, leading to a malacofauna of the western sites principally composed of species that are common in the surrounding matrix. One exception is *V. moulinsiana.* This snail represents a threatened relic from the early Holocene in the Central European landscape, but it is not an exclusive fen inhabitant. Besides, it has penetrated into the target area in the recent period, during the largest Walachian colonization *ca.* 650 years ago, from lowland refugia situated southwards (Horsák & Hájková, 2005). The western sites have been colonized from the identical non-fen species pool, which caused the higher frequencies of ubiquitous species, especially as compared with the eastern sites. The markedly higher share of forest species is a reminiscence of the previous forestation of these sites. This feature of snail assemblages reflects the fact that fens in the western region present isolated fragments within a more or less wooded landscape. On the contrary, the fen sites in the eastern region (the Inner Carpathians) are clear palaeorefugia in terms of their modern biota. As mentioned above, we assume only a few of them are palaeorefugia *in situ.* These sites are refugia for both plant and snail species and certainly for their communities as well. The occurrence of exclusive fen inhabitants and their relative high frequencies and abundances are characteristics of Inner Carpathian snail assemblages. A high historical age of the fen biota results in the existence of fen specialists within plants and snails mutually correlating in their occurrences. The fen snail specialists, whose distributions were significantly correlated with some plants to a higher degree than with any other snail, were completely or nearly completely limited to the eastern sites. According to palaeontological evidence they are glacial relics (see below).

We assume that the discovered biogeographical gradient within the Western Carpathians is not unique. Floristic data from other parts of the Alpine–Carpathian orogenic belt imply a wider distribution of this phenomenon. In the Rumanian Carpathians, the plant communities corresponding to our Inner Carpathian calcareous fens (ER) with *Primula farinosa*, *Carex hostiana, Sesleria uliginosa* and *Schoenus nigricans* are rare, distributed in several valleys and basins, and are called glacial relics (Pop *et al.*, 1962; Morariu, Ularu & Danciu, 1985). The small spring fens on flysch bedrock, corresponding to our Outer Carpathian calcareous fens (WR) lack these refugial species (M. Hájek & P. Hájková unpubl.). The same pattern might also be detected in the Alps, but further investigations are needed.

Co-correlations of snail and plant species

The main variation in the correlation of individual snail and plant species occurrences explained by the age of habitats could be considered as quite suspicious. Why was the main ecological gradient from mineral-rich to mineral-poor fens, confirmed both in vegetation (Hájek *et al.*, 2002) and mollusc fauna (Horsák & Hájek, 2003), expressed only as the second PCA axis? The result suggests that concordances between plants and snails are governed even more by historical development than by ecological gradients. Historical processes have surely had strong and also analogical influence on both plants and molluscs. On the other hand, both groups of organisms also strongly reflect the mineral poor–rich gradient, although in different ways. Vegetation displays nearly a complete species turnover along the mineral poor–rich gradient (Malmer, 1986; Hájek, Hekera & Hájková, 2002; Tahvanainen, 2004). The size of plant species pool clearly differs between calciphytes and acidophytes (Ewald, 2003), but not so substantially as in the case of molluscs. Since molluscs need calcium for building their shells and for other physiological processes (Wäreborn, 1969, 1979), they reach higher abundance and species richness in calcareous areas including calcareous fens. Therefore, the number of snail species gradually decreases towards acidic fens (Horsák & Hájek, 2003). Only a few calcifuge snail species exist in the European malacofauna at all. The largest part of variation in snail assemblages concerns only extremely rich and calcareous fens where the majority of snail species live. However, these fen types present only a part of fen diversity along the mineral poor–rich gradient.

Characterization of relic snails living exclusively in fens

The snails *Vertigo geyeri* and *Pupilla alpicola* (characterizing fens in the eastern region) represent, based on palaeoecological evidence, relics from the late Glacial and the early Holocene (Ložek, 1964, 1992). *V. geyeri* is a boreo-alpine species, which is present in the Boreal, Alpine, Continental and Atlantic zones of Europe (Falkner *et al.*, 2001). It is more or less continuously distributed in northern Europe, mainly in Norway and Sweden (von Proschwitz, 2003), but also extending to the warm, Atlantic climate of western Ireland (Kerney, Cameron & Jungbluth, 1983). *V. geyeri* is listed among the threatened animals in Annex II of the European Union's Habitats and Species Directive (EUHSD). In Central Europe, this snail represents a relic from wet glacial periods (Ložek, 1992). *P. alpicola* is distributed in the Alps and Western Carpathians (Kerney, Cameron & Jungbluth, 1983). This species was more widely distributed during the cold periods of the Pleistocene when many different ecological forms occurred (Ložek, 1992). The modern form of this snail has existed since the late Glacial. In the Western Carpathians this species represents a threatened glacial relic.

CONCLUSIONS

The studied snail assemblages express the same geographical pattern as vegetation, and we found snail species that display a similar distribution pattern to certain plant species. The classification of snail species based on probabilities of their co-occurrence with plants also follows the geographical gradient, which is not caused by any recent ecological dissimilarity of both areas. An important fact is that snail species with the highest probabilities of co-occurrence with plants are exclusive fen inhabitants and even glacial relics. Their distribution is nearly completely limited to the eastern region of our study area (i.e. the Inner Western Carpathians) where they represent a substantial part of the snail assemblages. Historical development seems to be one of the most important variable constituting qualitative characters of modern fragmented communities. On a small scale it can influence especially organisms with slower migration rate, such as molluscs or some vascular plants.

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